# Spalacosostea, an anomalous new terrestrial dryopid from South East Asia (Coleoptera: Dryopidae)

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Spalacosostea, an anomalous new terrestrial dryopid from South East Asia (Coleoptera: Dryopidae). - A new genus, Spalacosostea with two new species, S. loebli from Borneo and S. pselaphoides from Sumatra, is described. Both species were sifted from vegetation debris in rain forest. They are unusual for their small size and notable for sexual dimorphism, affecting the metathoracic wings and sensory organs. Females are wingless, with membranous metanotum, suboval elytra, vestigial eyes and short maxillary palps. Males have metathoracic wings well developed, metanotum well sclerotized and composed from several parts, large eyes, and their maxillary palps are very long and bear conspicuous peg-like sensilla. Taxonomically significant structures and morphological features unique to the Spalacosostea are discussed and illustrated. Diagnostic key to the species is given.

**Key-words:** Coleoptera - Dryopidae - *Spalacosostea* - Oriental region - Taxonomy - Morphology - Antennal sensilla.

# INTRODUCTION

The family Dryopidae, of almost world-wide distribution (BROWN 1981), presently consists of 240 species in 24 genera. They live in a variety of freshwater and terrestrial habitats. Many adults inhabit running waters and exhibit respiratory adaptive features, such as microplastron structures in *Pomatinus* Sturm, 1853 and *Elmomorphus* Sharp, 1888. In the contrary, the riparian dryopids (BARR & SPANGLER,1992), e.g. *Dryops* Olivier, 1791, *Pelonomus* Erichson, 1847 and *Onopelmus* Spangler, 1980, evolved macroplastron structures (HINTON 1969). Some of these species undertake dispersal flights and are often taken in great numbers in light traps. The few known larvae, are terrestrial or semiaquatic (BROWN 1987).

The entirely terrestrial groups, e.g. *Geoparnus* Besuchet, 1978, *Sosteamorphus* Hinton, 1936 and *Oreoparnus* Deleve, 1965, have been found in forest leaf litter and

flood debris. They are generally characterized by a very compact, heavily sclerotized, more or less ovoid body without plastron structures. Most of them lack metathoracic wings, have relatively small eyes, and their elytral striae are often strongly developed. Members of the Neotropical *Quadryops* Perkins & Spangler, 1985 were found in arboreal habitats, and those of the Indo-Malaysian Sostea Pascoe, 1860 were beaten from the foliage of different plants in rain forests (Kodada, unpublished). The arboreal dryopids may be roughly distinguished from the epigean ones by the more elongate body, the presence of large eyes, the well-developed metathoracic wings and the elytra which often have a metallic shine.

To date, nine dryopid genera have been recorded from the Oriental Realm, two of which (*Geoparnus* and *Sostea*) are terrestrial.

Two species of an additional terrestrial dryopid genus have been found by I. Löbl, D. H. Burckhardt, D. Agosti and A. Smetana in northern Borneo and Sumatra. These unusually small epigean dryopids exhibit remarkable sexual dimorphism affecting particularly the metathoracic wings and the sensory organs.

#### MATERIAL AND METHODS

Members of following genera of terrestrial dryopids were studied: *Geoparnus setifer* Besuchet, 1978 - holotype:  $\delta$ , paratypes:  $1 \, \delta$ ,  $1 \, \circ$  (MHNG); *Geoparnus* sp. - five undescribed species of both sexes (MHNG, CKB); *Guaranius carlosi* Spangler, 1991 -  $2 \, \delta \, \delta$  (NMW); *Sostea tuberculata* (Bollow, 1940) - holotype:  $\circ$  (RMS); *Oreoparnus microps* Deleve, 1965 - paratype:  $\circ$  (MHNG); *Protoparnus* sp. -  $\circ$  (CKB); *Sostea crassa* Hinton, 1936 - holotype:  $\circ$  (BMNH);  $\circ$  (CKB); *Sostea elmoides* Pascoe, 1860 - syntypes:  $\circ$  ( $\circ$  (BMNH), 2  $\circ$  (CKB); *Sostea hirtifera* Waterhouse, 1876 - holotype  $\circ$  (BMNH), M, F (CKB); *Sostea pilula* Grouvelle, 1898 - syntypes:  $\circ$  (BMNH),  $\circ$  (BMNH); *Sostea westwoodii* Pascoe, 1860 - syntypes:  $\circ$  (BMNH),  $\circ$  (BMNH),  $\circ$  (BMNH); *Sosteamorphus verrucatus* Hinton, 1936 -  $\circ$  ( $\circ$  4  $\circ$  (TMP); undescribed genus A from South Africa (Natal Middld., Doreen Clarck Nat. R.) -  $\circ$  (NMW).

Specimens used for morphological studies were relaxed in water, cleaned and treated with lactic acid. Metathoracic wings were removed, spread and observed on unmounted slides. For scanning electron microscopy specimens were dehydrated in graded ethanol series and air-dried from absolute ethanol, mounted on stubs with Tempfix and sputter coated with gold. Illustrations were prepared with aid of a drawing tube, using temporary transparency mounts. The differentiation of the sensilla is based only on the form and size of their cuticular parts. The terminology of the metathoracic wing structures follows Kukalová-Peck & Lawrence (1993).

# **ABBREVIATIONS**

BMNH Natural History Museum, London CKB Kodada collection, Bratislava MHNG Muséum d' histoire naturelle, Genève MNHP Museum National d' Histoire Naturelle, Paris

NMW Naturhistorisches Museum, Wien RMS Naturhistoriska Riksmuseet, Stockholm

TMP Transvaal Museum, Pretoria

D Dendritic sensilla
DF Digitiform sensilla
P1, P2, P3, P4, P5
S1, S2 Styloconic sensilla
TL, TM, TS, T1, T2
EL EL Elytral length

El Elytral index, ratio of elytral ML to combined MW of elytra

HW Width of head with eyes

LPE Medial length of pronotum and elytra

ML Medial length MW Maximum width

OI Ocular index, ratio of HW to minimum distance between eyes

Ø Mean value ± standard deviationn Number of measured specimens

### SYSTEMATIC SECTION

# Spalacosostea gen.n.

(Figs 1-65)

Type species: *Spalacosostea loebli* sp.n. Gender: feminine.

Etymology: The generic name is a combination of names Spalax (Spalacidae: Rodentia) and Sostea. Spalax are short-legged mammals that are extensive burrowers, characterized by the absence of external openings for eyes, although small eyes are present beneath the skin (referring to the vestigial eyes of females from the genus described below). Sostea is a dryopid similar to the new genus.

Diagnosis: Spalacosostea may be distinguished from all other described dryopids by following features in combination: (1) antennae six-segmented, pectinate with enlarged antennomere 1; (2) eyes in female vestigial; (3) male maxillary palpus with terminal segment unusually large, bearing conspicuous peg-like sensilla with an enlarged, sharply tipped apex on almost entire surface; (4) metathoracic wing with highly reduced anal veins; (5) tarsi four segmented.

The wingless female with membranous metanotum, suboval elytra, short maxillary palps and vestigial eyes, differ conspicuously from male. The male is characterized by the well sclerotized metanotum composed from several parts and developed metathoracic wings, elongate elytra, large eyes and very long maxillary palps with conspicuous sensilla. The association of both sexes is based also on similar: (1) types and distribution of the sensilla on the antennae, labium, labrum and legs; (2) shape of the labrum, labium and maxillae (maxillary palps excepted); (3) type of the macro- and micropunctation; (4) vestiture; and (5) both sexes of each species were found in the same samples.

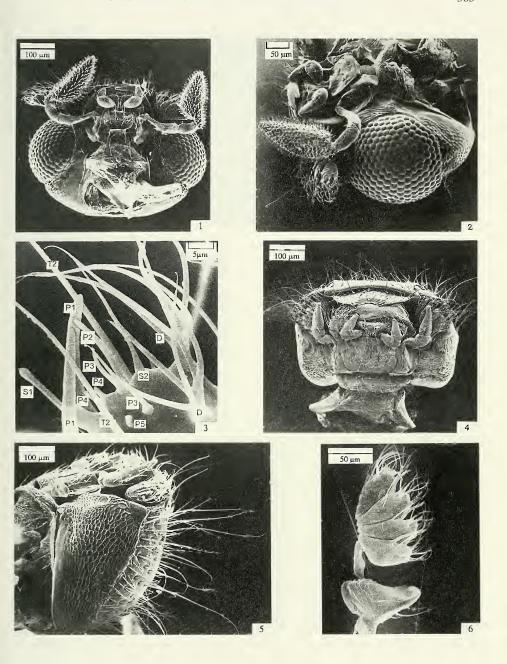
Description &: Body form elongate (Fig. 49), slender, moderately convex dorsally; about 2.4 times as long as wide (LPE/MW); length 1.20 - 1.60 mm (LPE). Colour in both sexes varies from yellowish-brown to brown with yellowish antennae and legs (obviously depending on maturity).

Vestiture of dorsal surface (Figs 19, 26, 35) consisting of three types of yellowish hair-like sensilla. Type TL = very conspicuous, erect, about 200 - 300  $\mu$ m long, arising from more or less deep, indistinctly bordered sockets; longest sensilla (TL) inserted on lateral elytral and pronotal margins. Type TM = intermediate, about 100 - 170  $\mu$ m long, erect, arising from shallow socket; longest sensilla (TM) situated on pronotum and elytra. Type TS = short, thin, about 40 - 70  $\mu$ m long, recumbent and arising from shallow inconspicuous socket. Ventral surface with similar hair-like sensilla as dorsal surface, but sensilla (TL, TM) arise mostly from large, shallow and very distinctly bordered sockets (Figs 20, 23, 32). Some specimens covered with encrusted material on cuticle of vertex and pronotum.

Head (Figs 1, 2, 26, 27) hypognathous, flat ventrally, arched dorsally and laterally; occipital area distinctly shorter than longest eye diameter; moderately retracted into prothorax. Punctation consisting of setigerous micro- and macropunctures. Micropunctures (sockets of sensilla TS) mainly on vertex and near occipital ridge; distance between micropunctures about 0.5 times length of sensilla (TS). Macropunctures represent sockets of sensilla (TL, TM), deeper and broader near eyes than on frontoclypeus and separated by a distance of about 1 - 3 facet diameters. Eyes (Figs 1, 2, 26) large, more or less protuberant, circular, coarsely faceted and only with a few interfacetal sensilla (cf. type TM) on their dorsal half.

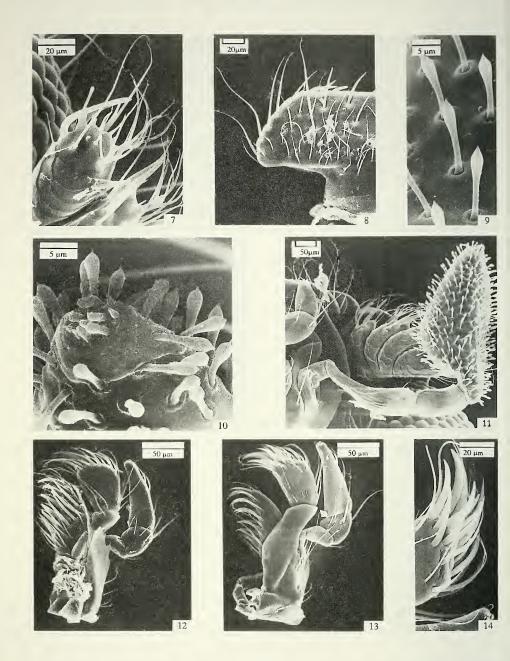
Labrum (Fig. 8) short (MW/ML = about 1.6), in posterior half strongly and abruptly constricted to third of MW and concealed by clypeus. Lateral tormal processes very short, bent ventro-mesally; postero-median process absent. Anterior margin more or less emarginate, with a few closely arranged, bluntly tipped, peg-like sensilla; lateral margin arcuate, with few hair-like sensilla. Epipharynx with two lateral fields of moderately long, mesally directed, recumbent hair-like sensilla (about as type TS), and postero-mesal rows of short and very closely set setae bordered laterally by flat, broad setae. Anterior margin of clypeus arched, with a flat ridge; frontoclypeal suture absent.

Antennae (Figs 3, 6, 7, 51) inserted into deep antennal sockets, six-segmented, microreticulated. Antennomere 1 robust, dilated distally, dorsally with sensilla TM and one sensillum TL; latero-dorsal margin with flat ridge adjacent to clypeal ridge in repose. Antennomere 2 as long as previous one, cylindrical and constricted in basal third; antennomeres 3 - 6 dilated anteriorly, approximately of same length. Sensory fields located on antero-median extension of each flagellar antennomere. Terminal antennomere (Fig. 3) contains greatest number of different types of sensilla: (1) hairlike sensilla type T1 = about 20 - 35 µm long and 1 µm wide at base; lateral and dorsal face with 6 - 8 sensilla T1; (2) type T2 = about 60 - 100  $\mu$ m long and about 2 -3 µm wide, finely longitudinally grooved, one subapical sensillum T2, bilaterally symmetrical on each side of the midline; (3) styloconic sensilla type S1 = approximately 30 µm long and 4 - 5 µm wide (MW), bluntly tipped peg inserted at tip of cylindrical projection, medio-dorsal face bears one subterminal sensillum S1; (4) type S2 = about 10 μm long and 1 μm wide, slightly bent, sharp tipped conical peg inserted on broad, short, basal projection, each antennomere bears only one median sensillum S2; (5) peg-like sensilla type P1 = approximately 35 - 40 μm long, 4 - 5 μm



Figs 1-6

Spalacosostea loebli sp.n.: 1, head of male, ventral view, 2, lateral view, 3, sensilla of the terminal antennomere, 4, head of female, ventral view, 5, lateral view, 6, antenna of male.



Figs 7-14

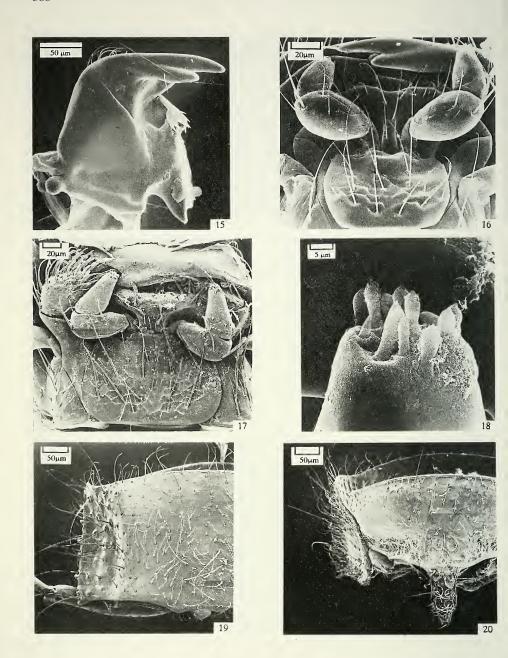
Spalacosostea loebli sp.n.: 7, terminal antennomere, male; 8, labrum, dorsal view; 9, sensilla of the maxillary palpus, male; 10, apex of maxillary palpus, male; 11, maxillary palpus, male; 12 maxilla of female, ventral view; 13, dorsal view; 14, apex of galea.

wide, slightly bent, bluntly tipped, two sensilla P1 inserted without a socket posteriorly to sensilla T2; (6) type P2 = one 25 - 30  $\mu$ m long, about 3  $\mu$ m wide, bluntly tipped peg without socket inserted sublaterally on dorsal face anteriorly to sensillum P1; (7) type P3 = about 10  $\mu$ m long, 1  $\mu$ m wide, thin, bluntly tipped pegs, without socket, one median sensillum P3 before sensillum S2 and two P3 laterally to S2; 8) type P4 = about 5  $\mu$ m long, 1  $\mu$ m wide, 0 or 2 sensilla P4 present on mediodistal area before sensillum S2; (9) type P5 = only one, very short conical peg about 2  $\mu$ m long and 1  $\mu$ m wide, inserted on dorsal face near lateral sensillum P3; (10) dendritic sensilla (Perkins & Spangler, 1985), type D = conspicuous branched sensilla without socket, about 45  $\mu$ m long and 6  $\mu$ m wide at base, antennomeres 3 to 6 bear 1 or 2 sublateral sensilla D. Antennomeres 3 to 5 similar to each other in sensillar distribution, but lacking sensilla S1, P2, P3, P4, and number of sensilla T1 reduced compared to antennomere 6.

Mandibles (Fig. 15) asymmetrical, short and broad, flattened dorso-ventrally, heavily sclerotized, with convex external margin. Ventral and dorsal surface glabrous; outer surface bordered dorsally by a distinct edge, moderately concave in proximal 0.66, microsculptured and with short hair-like sensilla. Right mandible with 4 teeth, dorso-proximal tooth very small; molar lobe strongly convex. Left mandible with three teeth and concave molar lobe. Prostheca (lacinia mobilis) hyaline, short, with closely inserted short spines. Each mandible bears many campaniform sensilla (PETRYSZAK 1977) and pore canal organs (ZACHARUK 1985) on teeth and in mola.

Maxilla with small cardo; stipes divided into small triangular basistipes and large elongated mediostipes; palpifer large, externally dilated into more or less broad lamina; both basistipes and palpifer with hair-like sensillum; mediostipes with several dorso-distal hair-like sensilla. Galea dorso-ventrally flattened, apically slightly dilated, about 0.5 times as long as mediostipes, with a few hair-like sensilla on ventral and dorsal side (mainly near base) and along external margin; distal region of galea bears a cluster of closely arranged, moderately bent stout setae. Lacinia triangular, flat, slightly shorter than mediostipes; dorsally and along internal margin with rows of strong bent setae; subapical external, dorsal and ventral submedian area of lacinia with several hair-like sensilla. Maxillary palps (Figs 11, 30) four-segmented, about as long as MW of head; segment 1 tiny; segment 2 more or less curved, distally dilated, about 4 times as long as segment 1 and about 1.6 - 1.9 times as long as segment 3; segments 2 and 3 microreticulated and with few short hair-like distal sensilla. Terminal segment expanded, robust, slightly shorter than length of two preceding ones combined, covered almost entirely with conspicuous peg-like sensilla with an enlarged, sharply tipped apex (Fig. 9). Terminal cluster of sensilla (Fig. 10) with bluntly tipped and distally enlarged pegs; conical, short, bluntly tipped pegs; and subterminal flattened, peg-like, partly sunken sensillum. Basal sensillar cluster (if present) consists of 4 peg-like, bluntly tipped sensilla.

Submentum short; mentum flat, with several hair-like sensilla (Fig. 16), lateral sides variably arcuate, lateral portion of anterior margin emarginate (Fig. 31), medial portion protruding; mental apodemes about as long as ML of mentum, narrow and bent distally. Prementum short and concealed by mentum, represented by a pair of



Figs 15-20

Spalacosostea loebli sp.n.: 15, mandible, ventral view; 16, labium, male; 17 labium, female; 18, apex of labial palpus, male; 19, pronotum of male, dorsal view; 20, ventral view.

sclerites. Palpus labialis three-segmented; segment 1 short, inconspicuous, without hair-like sensilla; segment 2 robust, about 1.8 times as long as wide (ML/MW), with inner side almost straight, outer side strongly convex, distal half with several short hair-like sensilla and long subapical external hair-like sensillum; segment 3 about as long as preceding, nearly conical. Apical sensory field (Fig. 18) similar to those on maxillary palpus, basal sensory field with two hair-like sensilla and digitiform (DF) sensillum (HONOMICHL & GUSE 1981). Ligula basally constricted, as long as prementum; antero-lateral portion rounded and laterally only weakly sclerotized; anterior margin medially more or less deeply emarginated; proximal half ventrally with two broad deep depressions on almost 0.8 of width of ligula; ventral surface bearing several hair-like sensilla and two bluntly tipped, bent, submedian peg-like sensilla near anterior margin; dorsal surface (hypopharynx) with short mesally directed hair-like sensilla in two pairs of sensory fields, each pair separated by a triangular area covered with longer, hair-like sensilla.

Dorsal tentorial arms long, thin and slightly surpassing middle of cranium; anterior tentorial pits not visible; posterior tentorial pits conspicuous; posterior tentorial arms joined by a transverse bridge, bearing two short bent and flattened processes. Gula short (MW/ML = about 4), trapezoidal, almost flat, finely microsculptured; gular sutures distinct. Occipital ridge (Fig. 26) fine, separating smooth dorsal surface from sculptured ventral parts. Occipital foramen large, in ventro-lateral angles articulating with apices of large cervical sclerites.

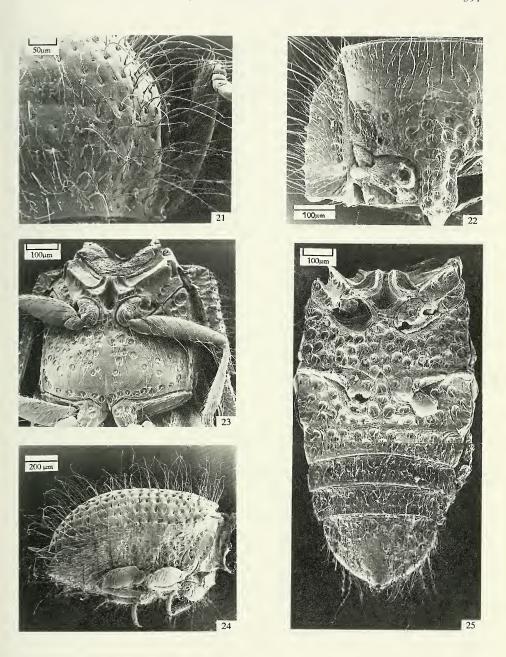
Pronotum moderately convex dorsally; with conspicuous longitudinal impression (Fig. 19) laterally; anterior margin arcuate, with a shallow emargination on lateral portions; lateral margin slightly arcuate or almost straight, finely crenulate and explanate; posterior angles almost rectangular; posterior margin trisinuate; central area usually with numerous sensilla (TS, TM), marginal areas mainly with sensilla TL. Internal posterior notal region bears two small condylles and a pair of ridges, latter fitting into cavities on anterior margin of elytra. Hypomeron (HINTON 1939) basally broadest, in apical third strongly narrowed (Fig. 20), with punctation variable. Prosternum bordered anteriorly by a flat ridge, rounded at antero-lateral angles and separated from hypomeron in distal fourth; about 0.5 times as long as wide in front of procoxae; strongly deflexed and finely, sparsely punctured in anterior third; remaining surface with large, flat bottomed punctures. Prosternal intercoxal process narrow (Fig. 20), about 2.4 times as long as wide, constricted and bluntly tipped in apical third; procoxal cavities open posteriorly; trochantin large. Mesosternum and mesepisternum concave anteriorly, glabrous; exposed part of mesepisternum with a transverse row of macropunctures anteriorly; mesepimeron with macropunctures; median mesosternal cavity deep, receives apex of prosternal process; mesocoxal cavities oval (dorsal view); mesosternal furca with slightly divergent arms. Scutellum small and subtriangular (MW/ML = 1), glabrous, with arcuate sides. Metasternum about 3 times as long as mesosternum (ML/ML), convex ventrally, without (Fig. 32) or with only very short, shallow longitudinal impression in posterior third (Fig. 23); median longitudinal endocarina present in posterior half; transversal suture (CROWSON 1967) absent, but its presumpted position marked by a transverse row of macropunctures;

metasternal intercoxal process apically emarginate, as long as wide. Macropunctures on lateral areas of metasternum and on long, exposed triangular area of metepisternum, but almost absent medially and on most of submedial-proximal areas of metasternum. Metendosternite with a long, narrow stalk; lateral arms and anterior tendons slender and short. Metanotum about 3 times as long as mesonotum; both divided into prescutum, scutellum and lateral scuta (LAWRENCE & BRITTON 1991); postnotum strongly transverse and slightly shorter than mesonotum.

Elytra elongate and parallel-sided in anterior 0.66, evenly arched towards apex (Fig. 35); flat dorsally in cross section, deflexed laterally; apices more or less acute (Fig. 36); anterior margin slightly elevated and finely crenulate; humeri prominent; sutural margin slightly elevated. Each elytron with 9 more or less regular rows of deeply impressed and densely arranged punctures (striae) between explanate lateral and sutural margin; striae 2, 3, 7 and 8 ending on elytral declivity, striae 5 and 6 ending before, striae 1, 4, 9 reaching apex. Strial intervals slightly convex, narrow; unpaired intervals with rows of sensilla (TL, TM), paired intervals bearing a double row of sensilla TS. Epipleura reaching elytral apex, about as wide as apex of tibia basally, narrowed apically (Fig. 32), oblique ventrally, more or less coarsely punctate and set with sensilla (TL) along finely denticulate lateral margin. Ventral elytral flange short and placed laterally slightly anterior to middle (Figs 36, 37, 38) near a "rubbing patch" (Crowson 1981).

Metathoracic wing (Fig. 56) about 2 times as long as elytron, slightly pigmented; apical field occupies almost 0.66 of wing; anterior margin composed of precosta (PC), costa (C) and subcosta anterior (ScA). Subcosta posterior (ScP) and darker pigmented radius anterior (RA) run parallel and close to anterior margin; both together form distally a radial bar ending abruptly, short before middle of wing; pigmented strips situated under radial bar. Radius posterior (RP) developed only in distal portion of wing being integrated into medial loop; radial cross-vein (r4) connecting presumed position of radial cell (incompletely bordered) with medial hook; posterior radial branches only slightly pigmented, broadened and flattened and not connected with RP. Media posterior (MP1+2) broad, dark pigmented and distally fused together with RP and cross-vein rp-mp2 to form medial hook; medial spur hardly distinguishable. All veins in medial field broadened, flattened, slightly pigmented and not reaching posterior wing margin; MP 3+4 short, forking into simple MP3 and MP4 fusing with CuA 1+2; cubitus anterior (CuA) forks into CuA1+2 and CuA 3+4; slightly pigmented spots remain from anal anterior and posterior sectors of anal veins.

Procoxae transverse, approximately cylindrical, about 3 times as wide as long; mesocoxae shorter, nearly conical; metacoxae transverse, with posterior excavation for reception of femora. Pro- and mesofemur about 1.5 times as long as procoxa; both broadest near middle; metafemur slightly longer than mesofemur, broadest basally, with straight dorsal and ventral outlines; all femora with short and long hair-like sensilla, longest sensilla in rows near dorsal and ventral face. Tibiae slightly longer than femora and 1.4 - 1.6 times as long as tarsi, apically and basally narrowed; pro- and mesotibia broadest closely posterior to middle, metatibia broadest approximately



Figs 21-25

Spalacosostea loebli sp.n.: 21, pronotum of female, dorsal view; 22, ventral view; 23, mesoand metasternum, male; 24, female, lateral view, head and prothorax removed; 25, meso-, metasternum and abdomen, female.

in middle; cleaning and smoothing fringe (SPANGLER & PERKINS 1989) absent; all tibiae with several types of hair-like sensilla in more or less regular longitudinal rows and few peg-like sharply tipped sensilla (Figs 46, 47). Tarsal formula 4-4-4; tarsal segments with few hair-like sensilla (Figs 41, 42, 57 - 59); claws moderately long, narrow, microreticulate; empodium without seta.

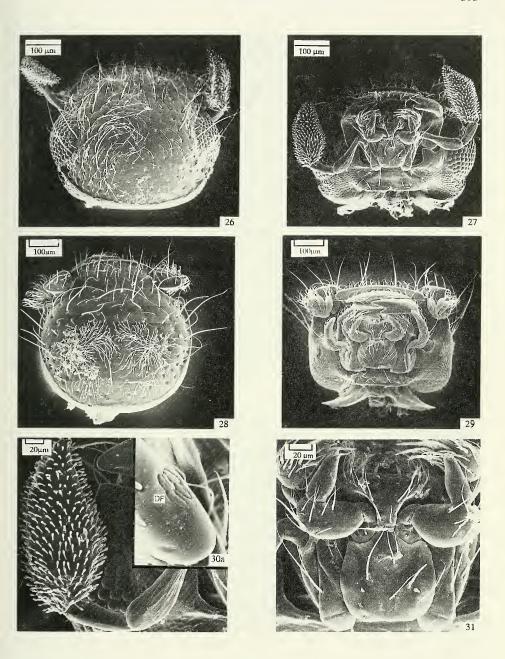
Abdomen with five slightly convex ventrites (Fig. 32), first two connate but separated by a distinct suture; ventrites 2, 3 and 4 about equally long; all with distinct laterosternites (KASAP & CROWSON 1975); intercoxal process about 1.25 times as long as wide (ML/MW). Tergites 2 - 7 with paired submedian fields of very short, densely arranged setae; tergite 7 bears posterior row of hair-like sensilla; pygidium with numerous hair-like sensilla. Seven pairs of functional spiracles situated in pleural membrane; spiracle 1 (Fig. 34) bears largest spiracular opening and filter apparatus with short spinules; spiracles 2 - 7 with shallow atrium, circular spiracular opening, prominent dorsal subatrial apodeme (RICHTER, 1969), short and bulbous ventral apodeme. Terminalia of all examined specimens only weakly sclerotized and hardly traceable, but similar to those in other dryopids. Aedeagus (Figs 43 - 45, 60 - 65) of trilobate type; penis long and slender, slightly curved, tapering apically; baso-lateral penile apophyses short; ejaculatory ducts inconspicuous; ventral membranous sac without sclerotized fibula. Parameres long, curved, tapering apically; phallobasis tubular.

*Description* ♀: Body form ovoid (Figs 33, 50), convex dorsally; body about 2 times as long as wide (LPE/MW); length (LPE) 1.30 - 1.70 mm.

Vestiture similar to those in males but sensilla longer and their sockets (mainly of TL and TM type) slightly deeper and broader.

Eyes vestigial (Figs 4, 5) and restricted to a small triangular field lying ventrally to cranial ridge. Labrum and mandible similar to those in male but mandible with rather convex sharp incisor edge. Maxillary palps only 0.4 times as long as MW of head, four-segmented (Figs 12, 13); segment 1 tiny; segment 2 longer, apically expanded; segment 3 slightly shorter than preceding; segment 2 and 3 with hair-like sensilla; terminal segment nearly conical, usually slightly longer than combined length of preceding segments and bearing: (1) apical sensillar cluster with several short, peg-like bluntly tipped sensilla, few short conical bluntly tipped pegs and one subterminal flattened peg-like and partly sunken sensillum; (2) basal sensillar cluster with several digitiform (**DF**) sensilla (Fig. 30b) and a round microdepression; (3) several hair-like sensilla (Figs 12, 13). Labium similar to that in male, but mentum shorter and broader (Figs 17, 29) with greater number of sensilla.

Pronotum convex dorsally, with feeble lateral longitudinal impressions; lateral margins basally more explanate and apically more arched than in male (Fig. 21); prosternal intercoxal process about 2.0 times as long as wide, medially slightly elevated (Fig. 22). Mesothorax as in male, but metasternum only about as long as mesosternum, without longitudinal and transverse sutures; almost entire surface of metasternum with deep macropunctures (Fig. 25); metepisterna weakly sclerotized and concealed by elytra (Fig. 24). Metanotum membranous (except for anterior margin of scuta) and not divided into distinct sclerites. Metendosternite (Fig. 48) Y-shaped, well sclerotized and its stalk about as longs as arms, anterior tendons absent.



Figs 26-31

Spalacosostea pselaphoides sp.n.: 26 head of male, dorsal view; 27, ventral view; 28, head of female, dorsal view; 29, ventral view; 30, maxillary palpus, male; 30a, basal portion of terminal segment of maxillary palpus, female; 31, labium of female.

Elytra (Figs 24, 33) suboval, about 1.4 times as long as their combined width; convex dorsally in cross section, strongly deflexed laterally; explanate lateral margin invisible in dorsal view; humeri not prominent; apices acute, strongly deflexed. Strial punctures large, dense, deeply impressed; unpaired strial intervals with rows of sensilla (TL); paired intervals with a single row of sensilla (TS). Ventral elytral flange, "rubbing patch" and metathoracic wings absent.

Legs (Fig. 24) in all parts shorter and broader that those in males but sensillar distribution similar.

Abdomen (Figs 24, 25) with ventrites similar to those in male, except for ventrite 5 bearing distinct apical shallow emargination, and tergites 2 - 7 lacking fields of short setae. Terminalia similar as in other dryopids (Lawrence, 1988): ovipositor (slightly longer than abdomen) consisting from laterally compressed coxites without styli; vaginal bursa without spines and sclerotized plates.

*Habitat:* specimens were collected by sifting vegetation debris mainly in primary *Lithocarpus - Castauopsis* and Dipterocarp forests.

# Spalacosostea loebli sp.nov.

(Figs 1-25, 39-48)

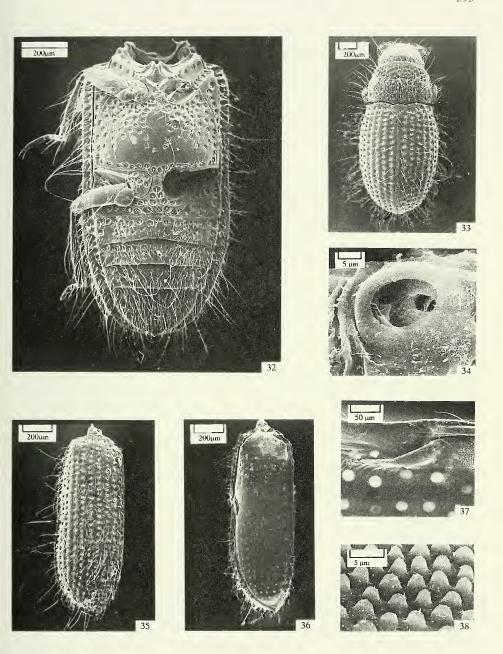
*Etymology:* this species is dedicated to my friend Ivan Löbl, who collected numerous new species of terrestrial dryopids during several expeditions to Southeast Asia.

Material examined: Holotype  $\eth$ : "SABAH: Poring Hot Springs, 500 m, 7. V. 1987 #15a Burckhardt - Löbl" MHNG; Paratypes:  $1 \circlearrowleft 4 \circlearrowleft 9$  with the same data as holotype, MHNG;  $2 \circlearrowleft \eth$ ,  $13 \circlearrowleft 9$ : same data but 6. V. 1987, MHNG;  $1 \circlearrowleft , 6 \circlearrowleft 9$ : same data but 11. V. 1987, MHNG;  $1 \circlearrowleft , 6 \circlearrowleft 9$ : same data but 13. V. 1987, MHNG;  $1 \circlearrowleft , 6 \circlearrowleft 9$ : same data but 550 - 600 m, 9. V. 1987, MHNG;  $4 \circlearrowleft \eth , 11 \circlearrowleft 9$ : same data but 600 m, nr Bat Cave, 10. V. 1987, MHNG;  $1 \circlearrowleft \eth , 31 \circlearrowleft 9$ : Borneo, Sabah, Mount Kinabalu National Park, Poring Hot Springs, area Kipungit Crk. 2, 14. - 30. VIII. 1988, A. Smetana lgt., MHNG, CKB;  $1 \circlearrowleft , 30 \circlearrowleft 9$ : "SABAH: Crocker Ra. 1600m, km 51 rte Kota Kinabalu-Tambunan, 18.V. 87 Burckhardt - Löbl 30a" MNHG, CKB;  $2 \circlearrowleft \eth , 4 \circlearrowleft 9$ : "SABAH: E Mt. Kinabalu 1150m, rte Ranau-Kota Kinabalu, 24. V. 1987 Burckhardt - Löbl 40" MNHG;  $1 \circlearrowleft 9$ : "SABAH: Crocker Ra. 1200m, km 63 rte Kota Kinabalu-Tambunan, 19. V. 87 Burckhardt - Löbl 31a" MNHG;  $5 \circlearrowleft 9 \circlearrowleft 9$ : "SABAH: Crocker Ra. 1270m, km 60 rte Kota Kinabalu-Tambunan, 17. V. 87 Burckhardt - Löbl 29a" MNHG.

Description of  $\delta$  from the type locality (#15a): length (LPE) 1.20 - 1.36 mm (Ø = 1.28 ± 0.05, n= 16), maximum width 0.52 - 0.56 mm (Ø = 0.54 ± 0.02, n= 16).

Cranial macropunctures very fine, their diameter distinctly shorter than facet diameter; eyes large (Fig. 2), HW = 0.42 - 0.49 mm (Ø =  $0.44 \pm 0.02$ , n= 16), OI= 1.57 - 1.88 (Ø =  $1.75 \pm 0.07$ , n= 16). Each flagellar antennomere with two dendritic sensilla (D); antennomere 6 characterised by insertion of three sensilla P3, two sensilla P4 and one sensillum P5 (Figs 3, 6, 7). Maxillary palps with segment 3 about 1.9 times as long as wide (Fig. 11); terminal segment bearing basal cluster of sensilla. Mentum broader than long (MW/ML= about 1.5), microreticulated (Fig. 16). Labial palps with short hair-like sensilla on segment 2 arranged in one more or less distinct row (Fig. 16), one or two sensilla sometimes inserted more basally; microreticulation on segment 2 present internally.

Pronotum 0.45 - 0.54 mm ( $\emptyset$  = 0.51 ± 0.02, n= 16) wide (MW), usually widest at basal fifth; lateral margin almost straight (Fig. 19); diameter of macropunctures



Figs 32-38

Spalacosostea pselaphoides sp.n.: 32, male, ventral view, head and pronotum removed; 33, female; 34, first abdominal spiracle, male; 35, elytra of male, dorsal view; 36, ventral view; 37, elytral flange, male; 38, rubbing patch, male.

distinctly shorter than facet diameter, macropunctures separated by a distance of about 1 - 3 facet diameters; punctures becoming sparser near anterior and posterior margins and larger laterally. Metasternum with short, indistinct median longitudinal impression (Fig. 23), glabrous area irregular (Fig. 23).

Elytra 1.76 - 2.08 ( $\emptyset = 1.85 \pm 0.08$ , n= 16) times as long as their combined width; strial punctures separated by a distance slightly smaller than their diameter; strial intervals dorsally slightly wider than diameter of one strial puncture, becoming smaller toward lateral margin.

Protibia (Fig. 46) about 1.45 times as long as protarsus; ratio (ML/MW) of tarsal segment 4 (Figs 41, 42): of protarsus about 4.0, of mesotarsus about 4.4 and of metatarsus about 4.7 (all measured in lateral view). Claws approximately 0.5 times as long as length of terminal tarsal segments.

Ventrites 1 and 2 with irregularly distributed macropunctures, ventrites 3 - 4 without or only with very few macropunctures; ventrite 5 always lacking macropunctures. Aedeagus (Figs 43, 44) with parameres about as long as phallobasis (lateral view).

*Description* of ♀ from the type locality (#15a): length (LPE) 1.26 - 1.46 mm (Ø = 1.39 ± 0.04, n= 43), maximum width 0.64 - 0.70 mm (Ø = 0.67 ± 0.02, n= 43).

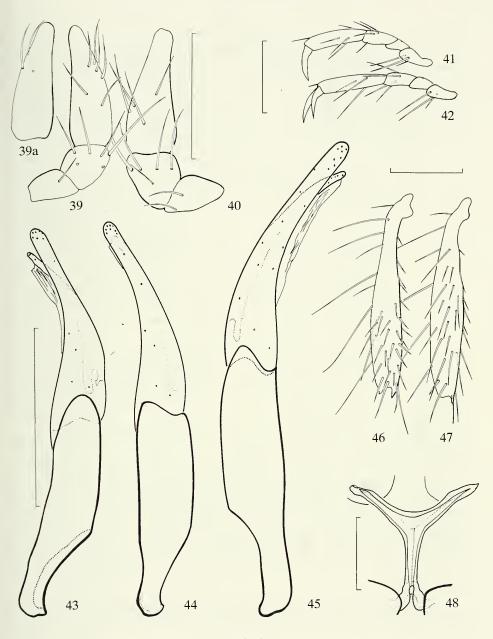
Cranial macropunctures distinctly larger than those in males, sensilla (TS) situated on vertex directed mesally. Antennal segment 6 without sensilla P3. Maxillary palps (Figs 4, 12, 13) with segments 2 and 3 approximately of same length, terminal segment 2.6 - 2.8 times as long as preceding, with 3 - 6 hair-like sensilla and a cluster of digitiform sensilla (DF) approximately in basal 0.2. Mentum (Fig. 17) about 1.5 times as wide as long (MW/ML), with microreticulation; labial palps as in Fig. 17.

Pronotum 0.57 - 0.66 mm ( $\emptyset$  = 0.61  $\pm$  0.02, n= 43) wide (MW), widest at basal third; lateral margin moderately arcuate (Fig. 21), macropunctures slightly larger than those on cranium and separated usually by a distance equal or slightly longer than their diameter. Glabrous area of metasternum very small (Fig. 25).

Elytra 1.36 - 1.58 ( $\emptyset$  = 1.46 ± 0.05, n= 43) times as long as their combined width; interstices more convex than in male.

Ratio (ML/MW) of tarsal segment 4: of protarsus about 2.5, of mesotarsus about 2.6 and of metatarsus about 2.8; claws shorter, broader and more curved than those in males.

Variation: Size and morphometric indexes see in Tables 1, 2. Both sexes are larger in higher altitudes; the aedeagi from these localities are also larger but their proportions are similar to those in males from lower altitudes (see Figs 43 - 45). Females exhibit minor variations also in number and distribution of sensilla on mentum, terminal segments of maxillary palps (Figs. 39, 39 a, 40) and segment 2 of labial palps.



Figs 39-48

Spalacosostea loebli sp.n.: 39a, terminal segment of left maxillary palpus, female from # 15a; 39, right maxillary palpus of the same female, basal segment removed; 40, female from # 40; 41, protarsus, male; 42, metatarsus, male; 43, 44 aedeagi of paratypes from # 15a, lateral view; 45, paratype from # 40; 46, protibia, male; 47, metatibia, male; 48, metendosternite, female. The scale bar represent 0.1 mm.

Table 1

Morphometrical characteristics of males *S. loebli* sp.n.

locality	n		MW of elytra	El	MW of pro- notum [mm]	HW [mm]	OI
30a	1 2	1.60	0,80	1.56	0.62	0.50	1.42
40		1.60	0.70, 0.72	1.66, 1,78	0.60, 0.65	0.50, 0.54	1.48, 1.42

TABLE 2

Morphometrical characteristics of females S. loebli sp.n.

locality	n	LPE [mm]	MW of elytra [mm]	EI	MW of pro- notum [mm]
29a	4	0.45 - 1.54 0.04	0.70 - 0.84 Ø= $0.76 \pm 0.06$	1.39 - 1.56 Ø= $1.43 \pm 0.13$	0.63 - 0.70 Ø= $0.65 \pm 0.03$
30a	27	0.60 - 1.78 $0.05 = 1.67 \pm 0.05$	0.77 - 0.84 Ø= $0.81 \pm 0.02$	0.37 - 1.60 0.06 0.06	0.69 - 0.76 Ø= $0.72 \pm 0.02$
31a	1	1.53	0.76	1.42	0.67
40	4	1.49 - 1.66 Ø= $1.59 \pm 0.07$	0.73 - 0.80 $\emptyset = 0.77 \pm 0.03$	0.45 - 1.53 $0.04 = 1.50 \pm 0.04$	0.67 - 0.70 Ø= $0.69 \pm 0.01$

# Spalacosostea pselaphoides sp.n.

(Figs 26-38, 49-65)

*Etymology:* from *Pselaphus* in reference to the unusual large maxillary palpi as in many pselaphids.

*Description* of ♂ from the type locality (# 11): Habitus (Fig. 49), length (LPE) 1.54 - 1.58 mm (Ø= 1.56 ± 0.01, n= 5), maximum width 0.65 - 0.67 mm (Ø= 0.66 ± 0.01, n= 5).

Cranial macropunctures with diameter about equal to facet diameter, separated by a distance of about 1 - 3 facet diameters (Fig. 26). Central area of vertex with more or less distinct cluster of sensilla TS with apices directed centrally. Eyes moderately large, HW = 0.43 - 0.47 mm ( $\emptyset$ =  $0.45 \pm 0.01$ , n= 5), OI= 1.36 - 1.41 ( $\emptyset$ =  $1.38 \pm 0.18$ , n= 5). Each flagellar antennomere with one dendritic sensillum (D); antennomere 6

characterised by insertion of two sensilla P3 laterally to sensillum S2 and by absence from sensilla type P4 and P5 (Fig. 51). Maxillary palps with segment 3 about 2.5 times as long as wide (Figs 27, 30); terminal segment without basal external cluster of sensilla. Mentum about as long as wide, without microreticulation (Fig. 31), on each posterior angle one short peg-like sensillum. Labial palps with short hair-like sensilla on segment 2 in two more or less distinct rows (Fig. 31); microreticulation absent.

Pronotum 0.56 - 0.58 mm ( $\emptyset = 0.57 \pm 0.01$ , n= 5) wide (MW), widest at base; lateral margin almost straight; diameter of macropunctures slightly longer than facet diameter, macropunctures separated by distance about equal their diameter; punctures becoming smaller and sparser near anterior and posterior margins; surface with numerous recumbent sensilla (TS) except for a small area along anterior margin. Metasternum without median longitudinal impression, glabrous area approximately triangular (Fig. 32).

Elytra 1.83 - 1.97 ( $\emptyset$ = 1.88  $\pm$  0.06, n= 5) times as long as their combined width; strial punctures separated by a distance distinctly smaller than their diameter; strial intervals dorsally about as wide as diameter of one strial puncture.

Protibia (Fig. 58) about 1.6 times as long as protarsus; ratio (ML/MW) of tarsal segment 4 (Figs 57 - 59): of protarsus about 3.0, of mesotarsus about 3.7 and of metatarsus about 4.0. Claws approximately 0.5 times as long as length of terminal tarsal segments.

Ventrites 1 and 2 with equally distributed macropunctures, ventrites 3 and 4 with macropunctures restricted onto anterior half; ventrite 5 with macropunctures near anterior margin. Aedeagus (Figs 60, 61) with short phallobasis; parameres about 1.3 times as long as phallobasis (lateral view), bluntly tipped, moderately bent ventrally (lateral view).

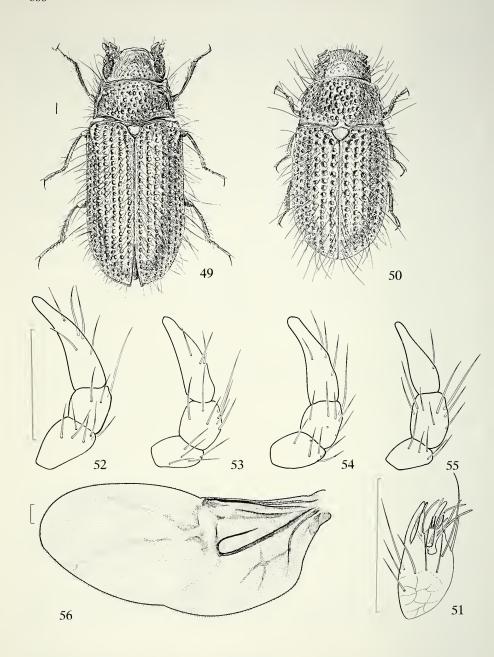
Description of  $\,^{\circ}$  from the type locality (# 11): Habitus (Fig. 50), length (LPE) 1.40 - 1.67 mm (Ø= 1.57  $\pm$  0.08, n= 30), maximum width 0.69 - 0.83 mm (Ø= 0.78  $\pm$  0.03, n= 30).

Vertex with numerous sensilla TS with apices directed to two sublateral points and form distinct clusters (Fig. 28). Antennomere 6 bearing, in addition to sensilla in male, one sensillum P5. Maxillary palps with segment 2 distinctly longer than segment 3, latter about as long as wide; terminal segment about 2.8 times as long as preceding, bearing 5 - 7 hair-like sensilla and a cluster of digitiform sensilla (DF) situated in basal 0.2 (Fig. 30a). Mentum about 1.4 times as wide as long (MW/ML), glabrous; labial palps as in Fig. 29.

Pronotum 0.63 - 0.71 mm ( $\emptyset = 0.66 \pm 0.03$ , n= 30) wide (MW), widest at basal third; lateral margin slightly arched; macropunctures coarse except those near anterior and posterior margin, separated usually by a distance smaller than their diameter, sometimes confluent.

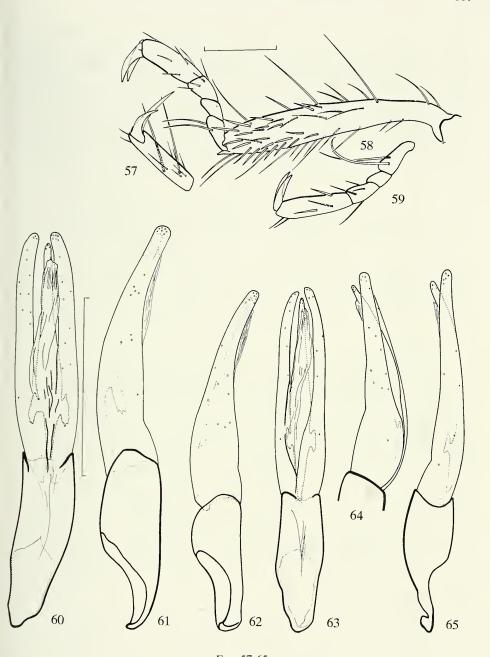
Elytra 1.41 - 1.59 ( $\emptyset$ = 1.47 ± 0.06, n= 30) times as long as their combined width.

Ratio (ML/MW) of tarsal segment 4: of protarsus about 2.2, of mesotarsus about 2.4 and of metatarsus about 3.3; claws shorter, broader and more curved than those in males.



Figs 49-56

Spalacosostea pselaphoides sp.n.: 49, male; 50, female; 51, terminal antennomere of female; 52, maxillary palps of females from #11, basal segment removed; 53, from #25a; 54, from #21; 55, from #7; 56, metathoracic wing. The scale bar represent 0.1 mm.



Figs 57-65

Spalacosostea pselaphoides sp.n.: 57, segment 4 of metatarsus, male; 58, protibia and protarsus, male; 59, mesotarsus, male; 60, aedeagus of paratype from #11, ventral view; 61, lateral view; 62, aedeagus of paratype from #21, lateral view; 63, ventral view; 64, 65, aedeagi of paratypes from #25a, lateral view. The scale bar represent 0.1 mm.

Variation: The specimens exhibit a moderate degree of variation in size, density of cranial and pronotal punctation as well as in morphometric indexes as shown in the Tables 3 and 4. The males vary moderately in the ratio of the parameral length to the phallobasal length, and in the shape of the paramere (see Figs 60 - 65); the specimens from lower altitudes are generally shorter and narrower with rather parallel-sided pronotum. The segments 2 - 4 of the maxillary palps and the segment 2 of the females labial palps exhibit differences in the shape, length and distribution of the sensilla (Figs 52 - 55). The eventual taxonomic significance of these variations is not understand. However, they indicate possibly only subpopulationnal isolation.

TABLE 3

Morphometrical characteristics of males *S. pselaphoides* sp.n.

locality n	1	LPE[mm]	MW of elytra [mm]	EI	MW of pro- notum [mm]	HW [mm]	OI
#21 2 #24 1	2	1.58 1.21 1.18 1.25 - 1.27	0.67 0.54 0.52 0.58	1.89 1.76 1.79 1.65 - 1.71	0.58 0.47 0.43 0.51	0.47 0.40 - 0.41 0.38 0.41 - 0.45	1.75

Table 4

Morphometrical characteristics of females *S. pselaphoides* sp.n.

locality	n	LPE[mm]	MW of elytra [mm]	EI	MW of pro- notum [mm]
#7	1	1.38	0.67	1.48	0.58
# 15 a	5	0.51 - 1.74 0.11 $0.11$	0.74 - 0.84 Ø= $0.81 \pm 0.04$	0.44 - 1.54 0.04	0.65 - 0.76 $\emptyset = 0.70 \pm 0.04$
#17	2	1.69 - 1.70	0.81 - 0.83	1.51 - 1.52	0.70
# 21	8	1.30 - 1.41 Ø= $1.35 \pm 0.03$	0.63 - 0.69 Ø= $0.66 \pm 0.02$	1.47 - 1.57 Ø= $1.52 \pm 0.03$	0.56 - 0.60 $\emptyset = 0.58 \pm 0.01$
# 25 a	6	0.30 - 1.52 0.07	0.72 - 0.76 Ø= $0.74 \pm 0.01$	0.32 - 1.51 0.07	0.63 - 0.69 Ø= $0.67 \pm 0.02$

# KEY TO THE SPECIES OF Spalacosostea

	· · · · · · · · · · · · · · · · · · ·
1	Body form elongate (Fig. 49); eyes large, well developed (Fig. 1); maxillary palps about as long as MW of head, with terminal segment robust, expanded (Fig. 11); humeri prominent (Fig. 35), metathoracic wings present; metasternum distinctly longer than mesosternum (Fig. 23). $\delta \delta \ldots 2$
-	Body form ovoid (Fig. 33); eyes vestigial, reduced to a very small triangular field (Fig. 5); maxillary palps 0.4 times as long as MW of head, with terminal segment nearly conical (Figs 4, 12, 13); humeri not prominent; metathoracic wings absent; metasternum about as long as
2	mesosternum (Fig. 25). ♀♀
-	Cranial macropunctures coarse, with diameter about equal to facet diameter (Fig. 26), pronotal macropunctures with diameter slightly longer than facet diameter (Fig. 49); each flagellar antennomere with one dendritic sensillum (D) (Fig. 51); segment 3 of maxillary palps about 2.5 as long as wide (Figs 27, 30); mentum as long as wide, glabrous (Fig. 31); segment 2 of labial palps with short hair-like sensilla arranged in two more or less distinct rows (Fig. 31); ventrites 3 - 4 with macropunctures in anterior half, ventrite 5 with macropunctures near anterior margin (Fig. 32); parameres about 1.3 times as long
3	as phallobasis (Figs 60 - 65)
_	Cranial and pronotal macropunctures coarse (Figs 28, 50); each flagellar antennomere with one dendritic sensillum (D); mentum glabrous (Fig. 29); segment 2 of labial palps with two rows of short hair-like sensilla; ventrite 3 - 4 with macropunctures in anterior half, ventrite 5 with macropunctures near anterior margin.  S. pselaphoides sp.n.

#### DISCUSSION

Spalacosostea shares the lack of the 2-nd cubito-anal cells with Quadryops and genus B, and the four-segmented tarsi with Quadryops. Sosteamorphus, Protoparnus, Oreoparnus and genus A lack metathoracic wings. The number of antennomeres is reduced in genus A to nine.

Spalacosostea, Guaranius, Sosteamorphus, genus A, Quadryops, Sosteamorphus, Oreoparnus and Protoparnus share the presence of dendritic sensilla on the flagellar antennomeres. These sensilla are variable in branching, and they are present also in some aquatic taxa. Their ultrastructural features and physiological functions are unknown.

*Protoparnus*, *Oreoparnus*, and genera A and B have lateral pronotal ridges while they are absent in *Sostea*, *Sosteamorphus*, *Geoparnus* and *Spalacosostea*.

In absence of detailed information on the morphology of *Holcodryops*, *Quadryops*, and genus B, all but the last known only as the single type specimen (SPANGLER 1987), the relationship of *Spalacosostea* (as other relationships within the family) remain unknown. However, no synapomorphy indicates close relationship of *Spalacosostea* with any other sympatric terrestrial group of the dryopids (*Geoparnus*, *Sostea*).

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#### REFERENCES

- BARR, Ch. B. & P. J. Spangler. 1992. A new genus and species of stygobiotic dryopid beetle, Stygoparnus comalensis (Coleoptera: Dryopidae) from Comal springs, Texas. Proceedings of the Biological Society of Washington 105 (1): 40 - 54.
- Brown, H. P. 1981. A distributional survey of the world genera of aquatic Dryopid beetles (Coleoptera: Dryopidae, Elmidae and Psephenidae sens. lat.). *Pan Pacific Entomologist* 57 (1): 133 148.
- Brown, H. P. 1987. Biology of riffle beeetles. *Annual Revue of Entomology* 32: 253 273.
- Crowson, R. A. 1967. The Natural Classification of the Families of Coleoptera. *Classey, Middlesex*, 187 pp.
- Crowson, R. A. 1981. The Biology of the Coleoptera. *Academic Press, London, New York*, 802 pp.
- HINTON, H. E. 1939. An Inquiry into the Natural Classification of the Dryopoidea, Based Partly on a Study of Their Internal Anatomy (Col.). The Transactions of the Royal Entomological Society of London 89: 133 - 184.

- HINTON, H. E. 1969. Plastron respiration in adult beetles of the suborder Myxophaga. *Journal of Zoology, London* 159: 131 137.
- HONOMICHL, K. & G. W. Guse. 1981. Digitiform Sensilla on the Maxillar Palp of Coleoptera III. Fine structure in *Tenebrio molitor* L. and *Dermestes maculatus* De Geer. *Acta Zoologica* 62 (1): 17-25.
- KASAP, H. & R. A. CROWSON. 1975. A comparative anatomical study of Elateriformia and Dasciloidea (Coleoptera). Transactions of the Royal Entomological Society of London 126: 441 - 495.
- Kukalova-Peck, J. & J. F. Lawrence. 1993. Evolution of hind wing in Coleoptera. *The Canadian Entomologist* 125: 181 258.
- LAWRENCE, J. F. & E. B. BRITTON. 1991. Coleoptera. In: Insects of Australia. Melbourne *University Press*, Vol.II.: 543 683.
- LAWRENCE, J. F. 1988. Rhinorhipidae, a New Beetle Family from Australia, with Comments on the Phylogeny of the Elateriformia. *Invertebrate taxonomy*, 1987, 2: 1 53.
- PERKINS, P. D. & P. J. SPANGLER. 1985. Quadryops, new genus, and three new species of arboreal Dryopidae (Insecta: Coleoptera) from Panama and Ecuador. Proceedings of the biological Society of Washington 98 (2): 490 - 510.
- PETRYSZAK, A. 1977. The sense organs of the mouth parts in *Libelula depressa* L. and *L. quadrimaculata* L. (Odonata). *Acta biologica Cracovieusia, Series: Zoologia* 20: 87 100.
- RICHTER, P. O. 1969. Spiracles of Adult Scaraboidea (Coleoptera) and Their Phylogenetic Significance. I. The Abdominal Spiracles. *Annals of the Entomological Society of America* 62 (4): 869 880.
- SPANGLER, P. J. & P. D. PERKINS. 1989. A Revision of the Neotropical Aquatic Beetle Genus Stenlielmoides (Coleoptera: Elmidae). Smithsonian Contributions to Zoology 479: 63 pp.
- Spangler, P. J. 1987. *Holcodryops mouli*, an anomalous new genus and species of beetle from Equador (Coleoptera: Dryopidae). *Proceedings of the Biological Society of Washington* 89: 616 621.
- Zacharuk, R. Y. 1985. Antennae and sensillae, pp. 1 69. *In*: Comprehensive insect physiology, biochemistry and pharmacology. Vol 6, Nervous system: Sensory (G. A. Kerkut & L. I. Gilbert eds). Vol. 6. *Pergamon press, Oxford*, 710 pp.